THE LIFE HISTORY AND HABITS OF CRYPTO-BRANCHUS ALLEGHENIENSIS.[1]

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(Contributions from the Zoölogical Laboratory of the University of Michigan, No. 109.)

I. Historical.

In spite of persistent attempts to work out the natural history of the giant salamander, *Cryptobranchus alleghenien**sis*, the habits, particularly the breeding habits, have remained little known. Very little has been learned about the development of the eggs, and the larvæ have not been described.

The first account is that of Townsend ('82) and consists of brief notes on the behavior and feeding habits, with a general description of some eggs deposited in August. McGregor ('97) described very briefly an embryo 16 mm. in length. Reese ('03) discussed principally the size, coloration, movements and feeding habits of the adults, and recorded his persistent attempts to obtain embryological material. In a later paper ('04), he gave the first accurate description of the unfertilized eggs.

Recently ('06[2]) I published a detailed description of the eggs and spermatozoa, and an account of the early stages of the development, with some incomplete observations on the breeding habits. The material for this paper was secured during the fall of 1905.

During the months of August and September, 1906, in north-western Pennsylvania, I devoted my entire time to the study of *Cryptobranchus*, with the object of securing a knowledge of its habits, and material for the study of its development. The purpose of the present paper is to record the results of this work so far as they contribute to a general account of the natural history of the animal.

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II. The Adults.

A. *Habits Not Peculiar to the Breeding Season.*

Habitat. — *Cryptobranchus* was found most abundantly in a large creek tributary to the Allegheny River, and the most favorable locality extended from its confluence with the Allegheny five or six miles up the stream.

The stream has a rather rapid descent, and a gravelly or rocky bottom. Shallow and rocky rapids make up the greater portion of its course, alternating with areas of deeper and more quiet

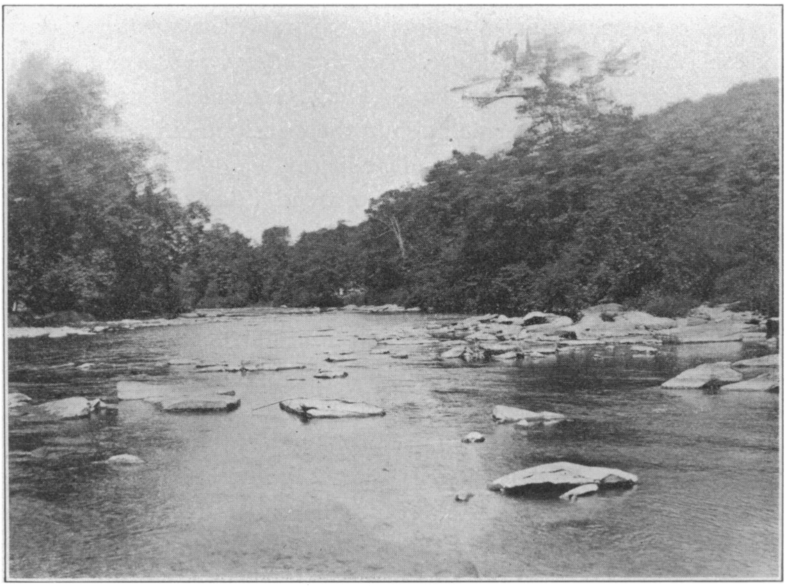


Fig. 1. Typical habitat of *Cryptobranchus alleghenienis.*

water. It is in the former situations (see Fig. 1) that *Cryptobranchus* abounds, lying concealed for the greater part of the time in crevices or caverns under large rocks in the stream bed. It is seldom that more than one individual is found under a rock, hence its life is in general a solitary one.

So far as my observations extend, *Cryptobranchus* comes forth but seldom in the day time, except during the breeding season. At night they venture abroad, perhaps in search of food; and fishermen who have speared by torchlight tell marvellous tales of the number of these creatures they have seen, usually lying quiet on the bottom when observed. According to Townsend ('82), in the early summer, when the water is clear, hellbenders are often seen on the bottom in considerable numbers ; in August he found them only under rocks. Presumably his observations were made by daylight.

The cavity or cavern used as a dwelling-place has the rock for its roof and the gravelly bed of the stream for its floor. In perhaps the majority of cases, ready-made caverns are chosen as homes, and these are reached by a natural opening. But the cavity often bears evidence of having been in part hollowed out by the animal, and is sometimes reached by a single burrow-like entrance, with a little heap of freshly excavated gravel at its mouth, on the downstream side of the rock. I have occasionally seen the front limbs used to scratch and push away sand and gravel, while the animal was forcing its way under a rock ; but the burrowing habit is only slightly developed. It is interesting to compare this beginning of the burrowing habit in *Cryptobranchus* with its marked development in the closely related but more terrestrial *Amphiuma.*

There is a striking similarity between the habitat of the American *Cryptobranchus* and that of the giant salamander of Japan (*C. japonicus* v. d. Hoeven, or *Megalobatrachus maximus* Schlegel), as described by Ishikawa ('04) ; but in the case of the latter the burrowing habit appears to be better developed.

Cryptobranchus does not thrive except in cool and shallow running water. When a specimen is placed in a tank of quiet water, it soon shows great uneasiness, swimming restlessly about as if seeking means of escape, and coming frequently to the surface for air. In a short time, as stated by Reese ('03), the stomach contents are regurgitated. So long as kept in such an unfavorable situation, it refuses food.

Size. — Although during the season I handled more than a hundred specimens, the largest adults of both sexes measured only 53 cm. in length. Townsend ('82) records the capture of some specimens 22 inches (56 cm.) long. The longest specimens obtained by Reese ('04) measured 55 cm. By far the greater number of specimens captured by me were much smaller than the extreme size given; specimens of about 35–40 cm. were apparently most numerous. The smallest sexually mature males measured about 33 cm.; females 35 cm.

Form. — The general form of the body (see Fig. 2) is such as to adapt it to bottom life, and to shallow crevices under rocks. The flattened head is wedge-shaped in a horizontal plane, enabling the animal to force itself into very shallow crevices. The fore limbs are adapted for ordinary locomotion, for climbing over rocks, and for use to a slight extent in burrowing.

As compared with the young, the adult is distinguished by the general looseness and wrinkling of the skin at the sides of the body, forming folds which become more prominent in adult life, and by the flaps of skin on the posterior sides of the limbs. During locomotion these folds and flaps undulate in the water, contributing to the uncouth appearance of the animal; they hang limp when the living specimen is taken out of the water, but become stiffened in preserved specimens.

Coloration. — Young adults vary but little in color or color pattern. The ground color is a dull brown, with conspicuous black spots and less conspicuous yellow spots, irregular in form and distribution, scattered over the dorsal and lateral surfaces. Since the coloration of the young adult is practically the same as that of immature specimens from 16 cm. upward, Fig. 14, from a specimen 26 cm. long, will serve to represent this stage, in which the spots are more conspicuous than in the young larvæ or the more mature adults. In older specimens (see Figs. 2–4) the general color effect may vary in two ways: it may become either greenish brown, or decidedly reddish brown. As stated by Reese ('05), these variations in color occur in both sexes.

The coloration of the dorsal surface is protective, closely resembling the gravelly bottom on which *Cryptobranchus* lives. The spots contribute largely to this general effect. When the stone under which a hellbender lies is overturned, the animal sometimes remains perfectly motionless, as if instinctively relying upon its coloration for protection. On account of its size, and the possession of various means of defense, it is probable that *Crypotobranchus* has few enemies, and its coloration is of value to it principally as a means of concealment while lying in wait for prey. The head, especially, resembles a flat stone covered with silt; when the animal is lying in a favorite position, under a rock with only the head exposed, it is extremely difficult to recognize it.

Locomotion. — The ordinary method of locomotion is by crawling slowly along the bottom. The limbs extend laterally and give little support, so that the abdomen lies in contact with the bottom. The order of movement of the limbs is the same as that of a trotting horse; the limbs which move together in the same direction are associated in diagonal pairs (Marey, '79). The pressure of the body on the ground is always diagonal; the body is supported and moved forward by a right fore foot and a left hind foot at the same time the other two limbs swing free from the ground and reach forward. The result is that the limbs on one side of the body are brought nearest together while those on the other side are extended furthest apart. The movement may be illustrated by two persons paddling a canoe, each with a long double-bladed paddle grasped by the middle; let one execute a stroke on the left hand at the same time the other makes the same movement on the right; let this performance be alternated with a similar one in which each person makes a stroke on the side opposite from that previously taken by him.

Cryptobranchus is also a good swimmer. In swimming the body undulates in a horizontal plane, like that of an eel, and the tail shares in this motion; in the most rapid swimming the motion of the tail is very vigorous, and is the principal means of propulsion. The legs, however, are of considerable use in swimming, both to propel and to guide the body and to preserve its equilibrium; during swimming at a moderate rate of speed the legs are the main propelling organs. The legs preserve their usual order of movement during swimming. Swimming is, then, effected by the combined motion of body, limbs and tail, the limbs playing a more important part in propulsion than the lateral fins of most fishes. Hence the swimming movements, as compared with those of fishes, present an advance toward those of most of the higher animals, which swim by the use of the limbs. *Cryptobranchus* often swims close to the bottom, so that locomotion is effected by a combination of crawling and swimming movements.

Breathing Movements. — The process of breathing by means of the lungs has been briefly described by Reese ('03); the following details may be added. In rising for air the anterior end of the body is stretched slowly in an oblique direction upward;

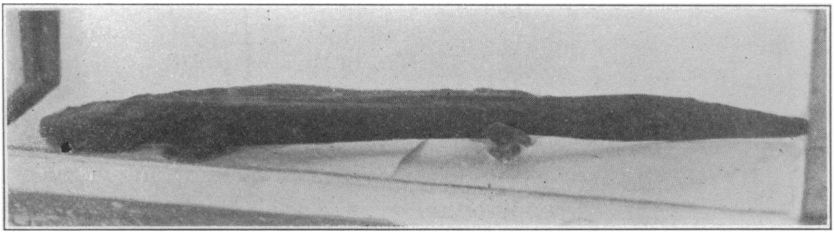


FIG. 2.

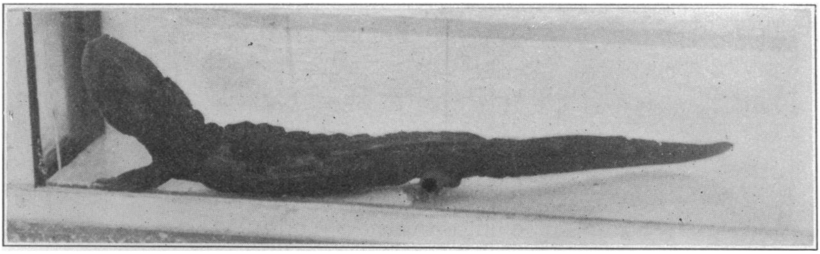


FIG. 3.

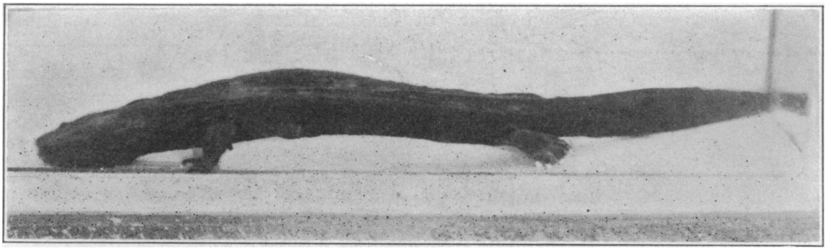


FIG. 4.

FIGS. 2–4. An adult female *Cryptobranchus allegheniensis*, 53 cm. in length. This specimen, full grown when captured, has been kept for seven years in an aquarium in the Zoölogical Laboratory of the University of Michigan. It is a trifle slender as compared with most newly-captured specimens. The white spots on the back are due to a recent growth of *Saprolegnia*.

FIG. 2. Normal resting position.

FIG. 3. Attitude when about to rise for air.

FIG. 4. Attitude when the lungs are fully inflated.

in shallow water the posterior end often remains under a rock. Fig. 3 shows an early stage of this movement. The air taken in through the nares at the instant the tip of the snout reaches the surface is probably immediately afterwards mixed with respired air expelled from the lungs; then the greater part of the mixed air is forced back into the lungs by a swallowing movement. The surplus air escapes through the mouth or gill slits as the animal sinks to the bottom; but enough air is forced into the lungs to elevate this portion of the body, giving the back an arched appearance (see Fig. 4). A little later, more of this air is expelled in order to enable the animal to resume its normal resting position (Fig. 2), and to prepare it for another inspiration.

According to Whipple ('06), the ypsiloid apparatus (see also Smith, '06 [1]) of many Urodeles subserves a hydrostatic function in changing the angle of inclination of the body in a vertical plane by pressing upon the posterior part of the expanded lungs and forcing the air forward. It is suggested that this may be the case with *Cryptobranchus*. But the animal makes active paddling movements with its forelimbs in rising to the surface for air; moreover when the lungs of a freshly killed specimen are inflated to the limit by means of a blow-pipe, their slender tips do not reach to the ypsiloid apparatus. Hence in the case of *Cryptobranchus* it seems impossible that the apparatus should have a hydrostatic function, excepting the slight effect produced by pressing the abdominal viscera forward.

Specimens in swiftly flowing water in cool weather rarely come to the surface to breathe. I have watched specimens that have remained motionless on the bottom for hours. On one occasion a dozen hellbenders in a covered creek aquarium built of wire netting to allow a constant current of water, were submerged by high water for two days without apparent injury. In these cases cutaneous respiration is probably sufficient; this may be aided by pharyngeal respiration, but in specimens confined in aquaria, having access to air, I have been unable to detect any current of water flowing in at the mouth and out at the gills, such as occurs occasionally in a resting *Necturus*. According to Gage ('91) the oral epithelium of *Cryptobranchus* is stratified and non-ciliated, as is usually the case with Amphibia whose respiration is mostly aquatic. The branchial slit is guarded at its pharyngeal opening by two valve-like flaps, in position and appearance like degenerate gills, which prevent the entrance of water from without. Their respiratory service, owing to their small size, is probably very insignificant.

Feeding Habits. — Examination of stomach contents shows that crayfishes form the principal food of *Cryptobranchus*; fishes are eaten only occasionally. Out of a dozen specimens examined in August, nine were found to contain crayfishes; only three contained fishes. *Cryptobranchus* sometimes takes a hook baited with earthworms, if cast near it. In captivity it will eat almost any small moving animal, or pieces of meat moved along a little to one side of the head. A specimen kept in an aquarium in the Zoölogical Laboratory of the University of Michigan is reported to have eaten frogs on several occasions, and once a toad. One of my newly-captured specimens seized a young *Necturus* about eight inches long, but soon released it. The adult *Cryptobranchus* will eat the eggs or larvæ of its own kind. Specimens kept in a creek aquarium in running water do not refuse food, even immediately after their capture.

Like many other amphibians, *Cryptobranchus* eats its own shed epidermis. The epidermis usually comes off in ragged pieces, giving the animal a tattered and uncouth appearance. The epidermis from the feet comes off like the fingers of a glove. The mouth is sometimes used to aid in the removal of the fragments. The practice of eating the shed epidermis is probably quite common amongst the Urodeles. I have observed a *Triton* (*Diemyctylus*) *viridescens* pulling off and eating the glove-like epidermis from the foot of another specimen. Ritter ('97) states that the shed epidermis of *Triton* (*Diemyctylus*) *torosus* forms an important article of diet for the animal.

Cryptobranchus apparently takes no notice of its prey until the latter approaches within a very few inches of its mouth and a little to one side, then seizes it by a remarkably quick sidewise movement. Perhaps the striking distance corresponds to the distance at which it can see clearly, or it may be the result of experience in catching wary prey. The enormous size of the mouth may compensate for the rather deficient eyesight (see

Reese, '05); it also makes possible the capture of rather large animals as food. No attention is ordinarily paid to pieces of meat unless they are in motion, or attract notice by actual contact. The rocks under which *Cryptobranchus* lurks also afford cover for its prey, hence a food supply may be obtained without leaving shelter.

Although I have handled the animals very often and without caution, I have never been bitten by them. A specimen confined in the Zoölogical Laboratory of the University of Michigan is said to have tried to bite several persons; this happened only after it had become accustomed to its surroundings and to the presence of people about it; probably it was only the usual feeding reaction, which had previously been inhibited by discomfort or fear.

Slime Production. — The surface of the body is at all times slimy enough to be extremely slippery, making the animal difficult to hold except when grasped by the neck. This constant secretion is of value to the animal in protecting the skin from abrasion in gliding over a rough rock, and perhaps also from parasites. But when a hellbender is injured or seized and forcibly held, an abundant flow of sticky, whitish, gelatinous slime, resembling the "milk" from the broken end of a milkweed stem, breaks out over the entire body or sometimes only from the tail. This slime causes a smarting sensation when it comes in contact with the freshly-cut surface of the skin.

Profuse slime production is at least indirectly a result of mechanical stimulation, though probably under the control of the nervous system, and associated with fear.

Reactions to Mechanical Stimuli. — The adult *Cryptobranchus* is strongly thigmotactic, seeking crevices under rocks or an angle of the aquarium in which it is confined — a result not entirely due to a negative reaction to light. It may even force its way under a stone of considerable size where no crevice exists, lifting the stone bodily in the water.

A shock or jar in the water sometimes causes a quick jerking movement, and withdrawal under a convenient cover; but the adult reacts far less readily to a shock than the larva.

When forcibly held, the animal wriggles actively, and sometimes makes a rather loud crackling sound, like that produced by boys who snap the joints of their fingers. The noise seems to come from the articulations of the vertebræ.

When tightly squeezed about the neck, the hellbender sometimes utters a shrill cry, perhaps due to the involuntary expulsion of air from the lungs.

Reaction to Light. — As previously stated, *Cryptobranchus* avoids the light. Like its thigmotactic response, this reaction is an important factor in its customary mode of life, since it usually seeks by day the cover of rocks where, concealed from possible enemies, it lies in wait for prey. Specimens confined in the laboratory are nocturnal in their activities, and during the day seek the darkest corner of the aquarium. According to Reese ('06), the tail is much more sensitive to light than the head or the middle part of the body. This may partly account for the favorite position of the animal — lying under a rock with only the fore part of the head exposed.

B. *Breeding Habits.*

Sexual Differences. — The adult male may be recognized (Reese, '04) by the presence of a swollen glandular ring or ridge of tissue about the opening of the cloaca. This is especially prominent in the breeding season, but may be recognized before the breeding season begins.

Females in the breeding season may be distinguished by the swollen appearance of the abdomen. As the egg-laying season approaches the eggs collect in the uteri, and when a ripe female is held in a vertical position with head uppermost, the lower portion of the abdomen sags and bulges out.

Females were found to be quite scarce or perhaps inaccessible as compared with the males. The ratio in those captured was about 1: 8.

Breeding Season. — As the time of the beginning of the breeding season was not accurately known, on August 11 I examined the reproductive tract of a newly captured male 34 cm. in length. The vasa deferentia were found to be contracted, about 2 mm. in diameter, and almost empty, containing only a very few spermatozoa, and these at the upper end. The spermatozoa were immotile. In the testes very few spermatozoa were mature.

On August 14 a large female was examined. The ovaries contained several hundred eggs almost fully developed, besides many smaller ones. The oviducts were empty.

Observations of this kind were continued throughout the month. On August 24 a female was found in which a few eggs had descended into the oviducts and become surrounded by a gelatinous envelope. This specimen was somewhat exceptional, as in others examined up to September 1 the eggs had not left the ovaries. Evidently there is considerable individual variation in the time when females ripen. On September 1 the first nest of eggs was found; these were in the first and second cleavage stages, hence had probably been deposited about 24 hours before. On September 3 a female was examined in which the eggs, surrounded by their gelatinous envelopes, had all collected in the lower part of the oviduct — the "uterus" — which was much distended, spindle-shaped, about 10 cm. long by 4 cm. in diameter at its widest part; its thin walls had a rich blood supply.

The preparations of the males for the breeding season proceeded at equal pace with those of the females. On August 31, in a specimen 38 cm. long, having the glandular region about the cloacal opening very much swollen, the vas deferens was found to be much distended with milt, and measured about 8 mm. in diameter. From this specimen the seminal fluid could be easily stripped. The spermatozoa were motile; the motion of the shaft is slow as compared with other forms, but that of the undulating membrane is rapid. The posterior third of the testis was darkened and shrunken, and appeared much degenerated; as stated by McGregor ('99), a wave of maturation begins at the posterior end of the testis and passes forward.

Hence the breeding season in this locality may be said to begin about the last of August. Possibly it is influenced by temperature; cool nights, accompanied by a marked decrease in the temperature of the water, set in three or four days previously. During the breeding season the temperature of the water ranged from 14° to 18° C. The egg-laying season lasts about two weeks.

Oviposition. — In a ripe female, the string of eggs in the uterus is aggregated in a much twisted and tangled mass. The egg capsules at the end of the uterus nearest the cloaca, hence those first formed, contain no eggs; likewise those nearest the oviduct proper, hence the last formed, are empty. The egg envelopes at this time are very soft, much wrinkled, contain no water and therefore fit closely about and between the eggs, taking up very little extra space. The number of eggs in a single uterus was counted in one specimen of average size and found to number 220; in another specimen of equal size 225. Those remaining in the ovary were very small (about 1–2 mm. in diameter), hence could not mature until another season. Therefore the number of eggs deposited by a female of average size in a single season must be about 450 — probably more in the case of a large female.

The strings of eggs after deposition are usually found twisted together in a tangled mass, corresponding to their condition in the uterus. The process of egg-laying was observed in aquaria in several instances. Egg-laying generally begins slowly, a short string of capsules containing from six to a dozen eggs protruding from the cloaca for many hours before the main mass is deposited; the majority of the eggs are deposited more rapidly, in a constant stream, the process requiring only about five minutes. The newly laid egg capsules take up water slowly, so that for a day or two the envelopes remain flaccid and much wrinkled. They gradually become plump and turgid (see Fig. 5) by osmosis, affording much more efficient protection to the eggs; the folding of the envelope almost entirely disappears. When the eggs are removed from the water, the egg proper looks much larger than it really is, because magnified by the spherical capsule at the bottom of which it lies.

As already recorded (Smith, '06[2]), of the two spawnings of eggs found during the autumn of 1905, one lot of eggs was in the open, the other partly under a rock. The eggs were not searched for under rocks at this time. In the season of 1906, about a dozen nests were found, all in cavities under rocks, and only a few scattering eggs were found in the open. Hence the deposition of eggs under rocks is the normal procedure, and their occurrence in the open quite exceptional. The "nest" of *Cryptobranchus* is simply the ordinary dwelling-place of the animal, used for spawning purposes.

The absence of black pigment in the eggs is probably correlated with the fact that they are laid in darkness. The eggs of *Necturus*, which are also laid under cover, are likewise devoid of pigment.

During the breeding season the water is unusually low. In one case a nest was found at the extreme water's edge, so that

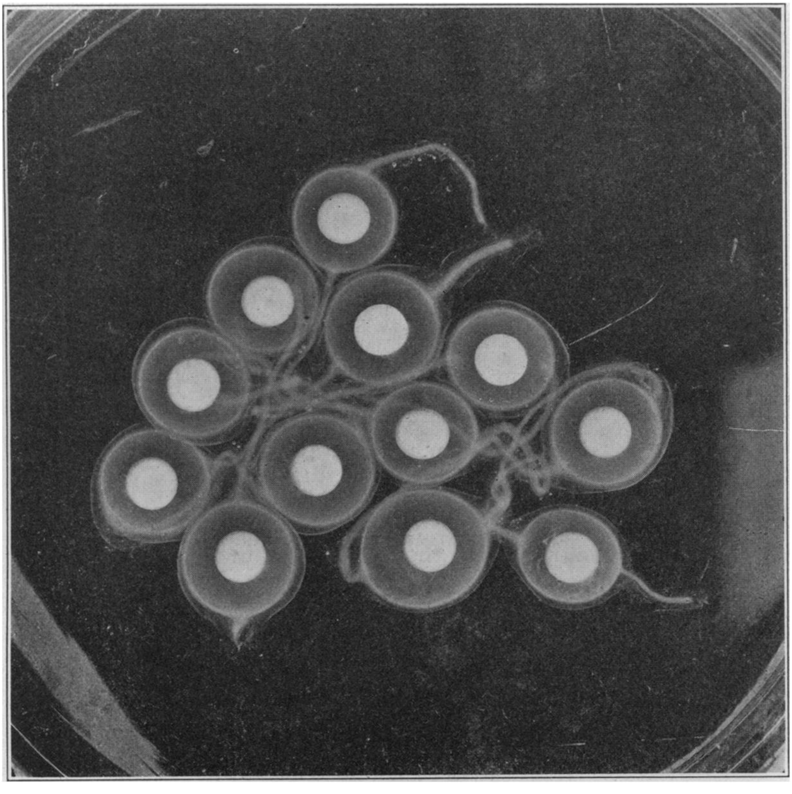


FIG. 5. Unfertilized eggs of *Cryptobranchus alleghenienesis*, after two days' immersion in water. Natural size.

the eggs were barely immersed, yet most of them were developing. In this way, by the periodical drying up of the water in swamps, may have originated the terrestrial nesting habits of *Amphiuma*, described by Hay ('88).

Fertilization. — In a previous paper ('06[2]), the conclusion was reached that fertilization in *Cryptobranchus* is internal. The evidence upon which this conclusion was based was afforded by the usual experiment of isolating a ripe female; an hour afterwards a few fertilized eggs were found, although their deposition was not directly observed. It was not known at the time that the female, as well as the male, devours the eggs of its own kind; moreover, the possibility of the regurgitation of the eggs, and their subsequent development, did not occur to me; yet this is undoubtedly what happened. The female *Cryptobranchus* is a voracious eater of the eggs of her own kind; digestion is very slow, and if the animal soon after eating fertilized eggs, is placed in quiet water, the eggs will be regurgitated without injury, and have been observed to continue their development. The number of eggs found on September 6, 1905, was rather large (estimated at about 80) to have been contained in the stomach at one time; but the female was an unusually large specimen, and the eggs must have been devoured before the inflation of their envelopes; hence the feat was quite possible. The evidence for internal fertilization cited above must be regarded as of no value.

The study of the breeding habits was begun with the expectation of finding spermatophores, such as are known to be deposited by *Triton viridescens* (Jordan, '91 and '93) and many other Urodeles (Wiedersheim, '00). Had such spermatophores existed it is quite probable that I should have recognized them through familiarity with spermatophores of *Triton viridescens*, deposited in aquaria, and observations (Smith, '07) on the spermatophores of *Amblystoma* studied in the field; yet, although strings of mucus containing spermatozoa were found floating in the water attached to rocks in localities where *Cryptobranchus* abounds, no spermatophores were found. The search for them was persistent and thorough, both under rocks and in the open, and in creek aquaria where the animals were breeding in large numbers; yet always with the same negative results.

Laboratory studies were conducted to shed light upon the process of fertilization. Eggs taken from ripe females uniformly failed to develop; no spermatozoa were found, either in the cloaca of the female or in eggs taken from the uterus. Females in the act of laying eggs were seized and some of the remaining eggs stripped from the cloaca; no spermatozoa could be found in them and they did not develop. The "opaque body" previously mentioned (Smith, '06 [2]), which can be dimly seen in the photograph (Fig. 5), was found to have no essential significance in the process of fertilization, since it is entirely a product of the female, and uniformly present in unfertilized eggs. As stated by McGregor ('99), the female has no seminal receptacle.

Tests were made in order to determine how long living spermatozoa would survive exposure to water. In seminal fluid taken from the vas deferens and thoroughly mixed with water, motion of the sperms, both of the shaft and the filament, continued for about 15 minutes. In drops of seminal fluid obtained by stripping and consequently mixed with the viscid secretion of the cloacal glands, the motion of the sperms continued for four hours after immersion in water.

Artificial fertilization was attempted on several occasions, always with complete success. Eggs for this purpose were secured by killing and cutting open ripe females. Three methods were followed: (*a*) "dry" fertilization — mixing eggs and milt together thoroughly, then immersing in water; (*b*) eggs and milt were placed simultaneously in water, then mixed together; (*c*) eggs were immersed in water for a minute or two, then milt added. All three methods were successful. In every case eggs not artificially fertilized were kept as a check; in no case did these develop. Hence it was proved that the sperms are able to penetrate the egg capsule from without, and that fertilization may take place after both eggs and sperms have been exposed to water.

All the evidence pointed to external fertilization, and it was sought to verify this by actual observation.

With the beginning of the breeding season a marked change took place in the behavior of the animals in their natural environment; they no longer remained secluded in hiding-places under rocks, but came out boldly by day, sometimes congregating in droves of from six to twelve, showing a social instinct quite lacking during the summer. As a rule they roamed restlessly about, poking their noses into crevices under rocks, as if exploring; sometimes, however, they lay quiet in the open. Several times they were observed to pile up in crevices between rocks, two or three lying alongside each other, or two or more at a time trying to force their way into the same crevice; this, however, may have been merely incidental to the favorable location. Those confined in aquaria were less shy than formerly, and paid little attention to the presence of an observer; this was true of newly captured specimens as well as of those that had been kept for some time.

Finally, in a large creek aquarium, under conditions made as natural as possible without affording too much cover, the com-

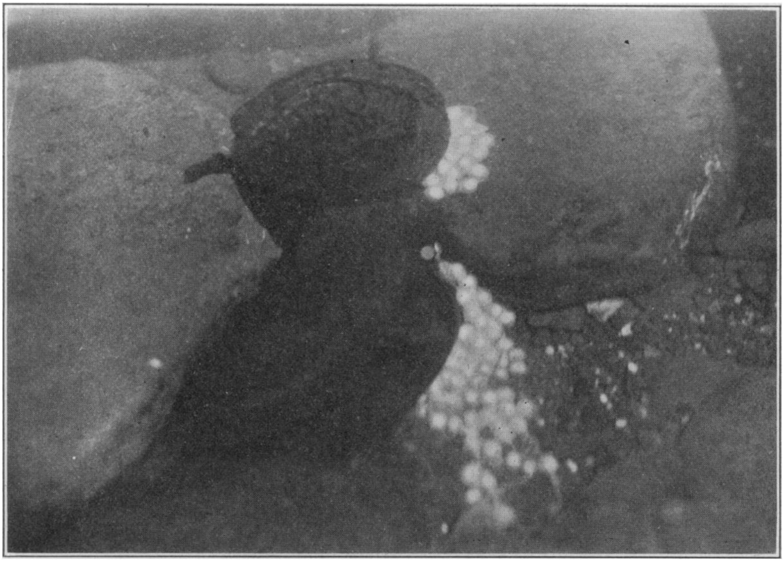


FIG. 6*A*. Photograph from under-exposed negative, showing spawningof *Cryptobranchus allegheniensis*. For explanation see Fig. 6*B*. The photograph was taken with the aid of a water-glass.

plete process of fertilization was observed at close range in two instances, while various details of the behavior of the animals during spawning were repeatedly observed. The process is essentially as follows:

The female, with a short string of eggs protruding from her cloaca, crawls restlessly about, dragging the eggs along the bottom; the male, whose attention seems to be attracted by the bright yellow eggs, follows her. Sometimes the female stops, and makes swaying lateral and vertical movements with the posterior part of the body. Finally she crawls partly (in the cases observed) under a rock, and egg-laying begins in earnest. During the remainder of the process of spawning the female lies quite motionless. The male moves to a position alongside and sometimes slightly above the female and overlying the eggs, or sometimes beside them. In this position, he makes swaying lateral and vertical movements of the posterior end of the body, raising and lowering it with his hind legs, much like a male *Triton viridescens* depositing a spermatophore, except that in the case

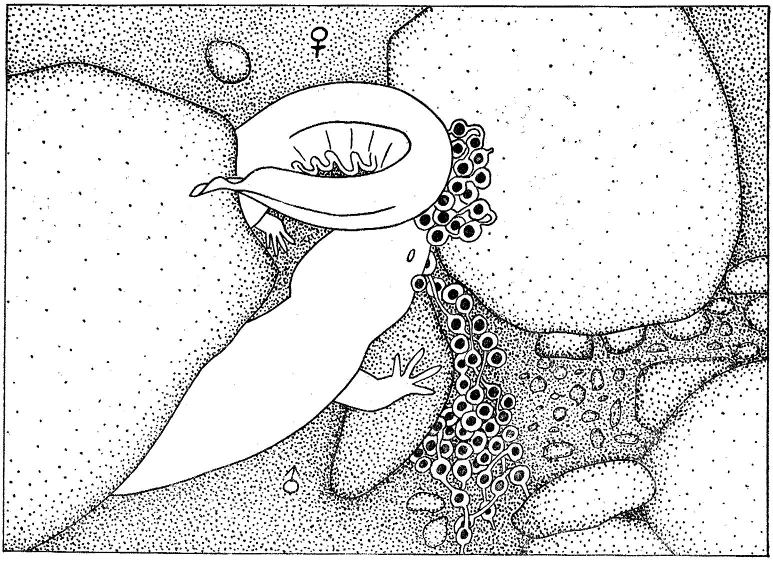


FIG. 6*B*. Drawing explanatory of Fig. 6*A*. The female, in a curved position has her head under a rock; the male, advancing from under the rock, with his foot on a stone, is not yet in position to fertilize the eggs.

of *Cryptobranchus* the motion is less violent. The movements also resemble those of the female preliminary to spawning. While executing these movements the male extrudes from his cloaca a snowy-white ropy or cloudy mass which consists of seminal fluid mixed with the secretion of the cloacal glands. On one occasion the deposit occurred in ropy chunks about 4 mm. in diameter and 2 or 3 cm. long. The deposit does not necessarily fall directly on the eggs, but sometimes on the ground beside them. Soon after, his own movements or those of other male hellbenders which approach brush the material about until it becomes diffused amongst the eggs. It usually happens that while a female is spawning several males are lurking about taking an evident interest in the proceeding. Once, while one male lay amongst the eggs (whether he fertilized them could not be seen) another male about a foot away, and certainly not in contact with the female, was observed to deposit milt. Evidently the excessive number of males is of value to insure fertilization. After fertilizing the eggs, the male sometimes leaves them, but more often remains beside them, or crawls under or amongst them.

Under perfectly natural conditions, spawning and the fertilization of the eggs takes place under large rocks where it cannot be observed; also the male more often remains with the eggs in the normal nesting place.

Photographs of the spawning operations were attempted with poor success (see Fig. 6).

Fertilization is then external as in most fishes, but the eggs are deposited without direct aid from the male. The presence of the string of eggs seems to be sufficient for sex recognition.

With the close of the breeding season, *Cryptobranchus* becomes more shy, avoids the light, and is seldom seen in the open.

Kerbert's account ('04) of the behavior of a pair of captive specimens of *C. japonicus* during spawning will be interesting for comparison. "Schon zu anfang des August 1902 verhielten sich die beiden Tiere anders als gewöhnlich. Wahrend die durchaus trägen, stumpfsinnigen Geschöpfe in der Regel tage- und wochenlang bewegungslos, fast wie tot, auf dem Bodén ihres Behälters lagen, nur äusserst langsam nach den ihnen dargebotenen Fischen schnappten, das Licht scheuten und immer die dunkelsten Stellen ihres Behälters aufsuchten, fingen dieselben im August an sich einander zu nähern und gegenseitig zu berühren. Manchmal wurden zitternde und wellenförmige Bewegungen des ganzen Körpers wahrgenommen.

Die Vermutung lag auf der Hand, dass ein Erregungszustand des Nervensystems als Einleitung zur Zeugung eingetreten war. Das Liebesspiel dauerte nur einige Tage. Eine eigentliche Begattung habe ich nicht beobachtet — und auch nicht erwartet." (Kerbert naturally expects fertilization to be accomplished by means of spermatophores). . . .

"Nachdem das grössere, oder — wie ich nacher festzustellen in der Lage war — männliche Tier (1 m. lang) schon seit Anfang September eine unverkennbare Unruhe gezeigt und im Sande am Boden seines Behälters eine deutliche Grube oder Vertiefung gewühlt hatte, fing am 19 September — es war ungefähr sechs Uhr Nachmittags — bei dem kleineren Tiere die Ablage der eigentümlichen Eiermasse an. . . .

Wahrend der Eiablage schwamm das Weibchen in merkbarer Unruhe herum, legte sich aber nach Beendigung dieses Vorganges ganz ruhig hinter den Felsen an der Hinterwand des Behälters. Das grössere Tier war vom Anfang an weit unruhiger und mehr aufgeregt als das Weibchen, schwamm fortwährend durch die von den heftigen Schwimmbewegungen beider Tiere allmählich in die sandige Grube geratene Eiermasse und wehrte die kleinen Fische, Mitbewohner des Behälters, mit geöffnetem Maule von den Eiern ab. Obwohl er sich einige Minuten später scheinbar ruhig bei der Eiermasse hinlegte, war die Erregung des Nervensystems doch offenbar eine so intensive, dass die Haut des Rumpfes und des Schwanzes wellenförmige, zitternde Bewegungen zeigte, ja dass sogar eine heftige Ejaculation von Sperma erfolgte. Eine schleimige grauweisse Masse machte das Wasser trübe. Bei mikroskopischer Untersuchung stellte sich unverkennbar heraus, dass in dieser schleimigen Masse eine grosse Anzahl von Samenfäden anwesend war. Mit voller Bestimmtheit war also nachgewiesen, dass das grössere Tier wirklich ein Männchen war." No deposit of material in a definite mass to form a spermatophore was observed. Kerbert rejects the idea that the emission of seminal fluid on this occasion indicated external fertilization of the eggs laid at that time, and suggests that the spermatozoa diffused in the water might be taken up into the female cloaca to fertilize the eggs for another season; or that the extrusion of milt at this time has no significance in fertilization, being merely incidental to the excitement of the male on account of the spawning of the female. Ishikawa ('04) also inclines to the belief that fertilization is internal, though without conclusive evidence. In view of the results obtained with *C. alleghenienis* it seems very probable that the observations cited above indicate external fertilization in *C. japonicus*.

Considering the low taxonomic position of *Cryptobranchus* amongst the Urodeles, the occurrence of external fertilization in this form indicates that this is the primitive method for the group; internal fertilization by means of spermatophores, characteristic of so many Urodeles, is a later development.

Nothing conclusive is known concerning the method of fertilization in the Crossopterygian Ganoids, the ancestral stock from which the amphibia are believed to be descended. In the higher Teleostomi, with a few notable exceptions, fertilization is external. In the Dipneusti, which, like the Amphibia, are supposed to be derived from a primitive Crossopterygian form, nothing definite is known concerning the manner of fertilization. In view of the diversity of habits within such groups as the Teleostomi and the Urodela, and the wide gaps between the Urodeles and the nearest living representatives of ancestral groups, it is probable that even were our knowledge of the habits of existing animals complete, a comparison between the Urodeles, the Crossopterygii, and the Dipneusti would have little phylogenetic significance. On the other hand, the occurrence of a simple method of external fertilization as the primitive condition of the Urodeles suggests the possibility of finding within the group stages in the development of the complicated breeding habits, involving internal fertilization by means of spermatophores, characteristic of most of its representatives.

Brooding Habits. — It has been noted previously that the male usually remains with the eggs after fertilizing them. That the male may render efficient protection to the newly-laid eggs is shown by the following incident of September 1, which I quote almost verbatim from my notes.

A large "red" hellbender (afterwards identified as a female) crawled across the stream toward a flat rock submerged in about 10 inches of water. This rock was about 3 feet by 2½ feet, slightly tilted so that the down stream side was a little raised from the bottom. As the female approached this rock, the large flat head of another *Cryptobranchus* (afterwards found to be a male) of unusual size was thrust out from under the down-stream edge of the rock and the newcomer was seized at the side of the head by the jaws of the male. She drew back and was released.

She went away a short distance but repeatedly returned and was repulsed in the same manner. Another small specimen (afterwards found to be a male) joined in the attack, but was also seized and repulsed; once he effected an entrance, whereupon a struggle ensued beneath the rock, as was shown by the water becoming turbid. The intruder withdrew.

The large female returned to the attack. She was seized with a firm grip, which lasted several minutes, during which the combatants rolled over and over, and sometimes drifted with the ventral surfaces uppermost. When released, the female swam away for a rod or more, and did not return.

The large male returned to the rock, but kept his head exposed, as if watching for another attack. Sometimes he held his head erect in an aggressive attitude like an angry snake, although it is possible that this was only a movement preliminary to rising for air. At my approach, he assumed this apparently threatening attitude, contrary to the usual custom in such cases of remaining motionless, or withdrawing under the rock.

All the specimens concerned were captured. The rock was overturned, and beneath it was found a cavity containing a large mass of eggs which were immediately swept down stream by the current. When collected they were found to number nearly 600, in first and second cleavage stages.

Another small male and a small *Necturus* were also found under the rock, but not in the cavity containing the eggs; they were on the side most remote from that occupied by the large male. Presumably their presence had escaped his attention, occupied as he was with his enemies.

The large male had a greatly swollen cloacal region, and his struggles when handled caused milt to exude from the cloacal opening. The stomachs of all the specimens excepting the small male found under the rock (the *Necturus* was not examined) were found to contain eggs; the large male contained 23 eggs, the female 22, and the small male 10. In the case of the female, strings of eggs protruded from the mouth and from the branchial aperture. Since the female was found by examination to be a spent one, and spent females at this date were rare, it is very probable that the eggs were laid by her. Even while I was gathering the scattered eggs, another hellbender appeared on the scene and attempted to devour them.

As previously stated, the eggs were in the first and second cleavage stages, and appeared to represent a single spawning. This was the first nest found during the season, and no other nest was found near it.

In the majority of nests found containing eggs in an early stage of development a male was present, a female never. In one case a male was found in a nest containing embryos two or three weeks old; but there is no certainty that he had remained there continuously during that time, or that the embryos were his own offspring.

The number of eggs found in the stomach of a single *Cryptobranchus* usually ranges from 15 to 25; in a few cases this number was considerably exceeded. The digestive processes of the hellbender are extremely slow, and I have taken undigested eggs from the stomach a week after they were eaten.

So far as observed, only recently laid eggs were eaten by the adults. After eggs have been laid several days they are rendered inconspicuous by a covering of silt.

As previously stated, the number of eggs usually deposited in a single nest is about 450 to 500. Nests found late in the season, with eggs in an advanced stage of development, contained nearly the full number of eggs; probably not more than a tenth part, in most cases, had been eaten.

We have here the beginning of a paternal brooding habit, but only the beginning. A male in making a valiant defense of the nest protects the eggs, to be sure, but at the same time he guards his own food supply. Thus in the case of *Cryptobranchus* the brooding habit may have its origin in the feeding habit. On account of the slowness of his digestive processes, and the short period during which, it appears, the eggs are available as food, the male hellbender alone is unable to eat more than a small portion of the eggs. The habit of defending the eggs during the early stages of their development is presumably, even though some of them are eaten, of advantage to the species; and this guarding habit may be initiated in connection with the feeding instinct.

In objection to this interpretation it might be urged that an animal that had just eaten would not be likely to quarrel over more food; but as a matter of fact the hellbender caught attempting to eat the scattered eggs was already gorged with them.

Another possible interpretation demands consideration. In the case described, the male may have been merely holding the nest while awaiting the coming of another ripe female. The hellbenders driven away were all males with the exception of a spent female; there was no opportunity to observe the reception of a ripe female by a male guarding eggs. Evidently further observations are needed to supply conclusive evidence of the origin of the brooding habit.

The aggressiveness displayed by the male *Cryptobranchus* in defending the nest is the first instance I have observed of pugnacity on the part of a Urodele. In these contests over the possession of the nest, the male doubtless has an advantage over a spent female, since the latter seems to be in a weak condition immediately after spawning.

Concerning the brooding habits of *C. japonicus*, Kerbert ('04) says: "Nach Beendigung der Eiablage legte sich das Weibchen offenbar in grösster Ermattung in eine Ecke des Behälters hin und kümmerte sich um das Gelege gar nicht mehr. Das Männchen hingegen hat seitdem die Eiermasse nicht verlassen — ja sogar *die Brut fortwährend bewacht*. . . . Denn sobald das Weibchen der Eiermasse zu nahe kam, stürzte das Mannchen in sichtbarer Wut auf die Mutter los und vertrieb sie . . . kriecht der Männliche Riesensalamander zwischen den verschiedenen Strängen der Eiermasse hindurch und bleibt dan von der Eiermasse umhüllt liegen, oder er legt sich einfach neben die Eiermasse hin. In beiden Fällen aber hält er, hauptsächlich durch eine pendelartige Bewegung des ganzen Körpers, von Zeit zu Zeit die ganze Eiermasse in Bewegung. Durch diese Bewegung entsteht eine für den Atmungsprozess der Eier und Embryonen höchst wichtige Wasserströmung, während die Lage der Eiermasse hierdurch gleichzeitig fortwährend wechselt."

III. The Embryo.

An abundance of fertilized eggs was collected, but on account of the lack of proper facilities great difficulty was experienced in keeping the material alive long enough to secure a complete series. By far the greater part of the eggs perished from variations in temperature, insufficient aeration, or the attacks of water-mold, and it was only by constant search for new nests that the later stages were obtained.

Segmentation.—The segmentation stages have already been described (Smith, '06[2]), and since I expect to make a detailed study of the embryology the subject of a special paper, only a few brief notes on the development of the embryo need be given here.

In artificially fertilized eggs the first cleavage furrow appears about 18 hours after fertilization. Segmentation proceeds with increasing rapidity, varying with the temperature, and in a few days a blastula is formed having a shallow segmentation cavity with a very thin, almost transparent roof. So far as external changes visible to the unaided eye are concerned, development during the latter part of this process is comparatively slow. It is also a critical period in the development of the egg; more embryos die at this time if exposed to slightly unfavorable conditions than at any other.

Gastrulation commences in from six to ten days, according to temperature, after fertilization. The blastopore is formed much as in the frog's egg. The process is quite rapid after the appearance of the short deep horizontal groove just below the equator; this groove quickly elongates, becomes crescent shaped, and the horns close to form a complete circle in some eggs, while in others of the same lot subjected to the same conditions, the process of gastrulation has just begun. The yolk plug rapidly diminishes in size.

Origin of the Nervous System.—The broad but shallow neural groove appears at about the time the circle of the beginning blastopore is nearly complete—a day or two after gastrulation commences. A few hours later the neural folds appear as a sharply-defined horse-shoe shaped ridge about the upper end of the neural groove; the arms extend downward and closer together until they reach the dorsal lip of the blastopore, which by this time has narrowed to a very small circle. The development of the neural folds proceeds rapidly until their closure a day or two after their first appearance.

Eighteenth Day Embryos. — In from two to three weeks after

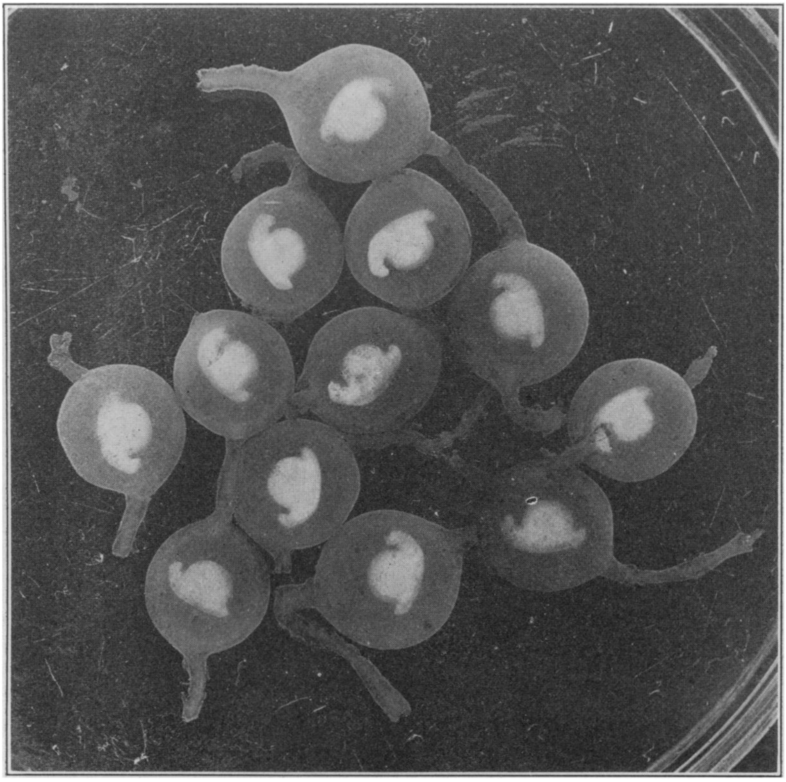


FIG. 7. Embryos of *Cryptobranchus allegheniensis*, about 18 days old, within egg capsules. Natural size.

fertilization the embryos reach the condition represented in Fig. 7. At about this time the rudiments of the external gills appear. A broad horizontal pink band along the left side of the yolk sac indicates the beginning of the vitelline vein. The dorsal surface becomes slightly pigmented, the pigment spots being grouped metamerically (cf. McGregor, '97). The embryos squirm slightly when placed in the fixing fluid.

Observations in the field were necessarily discontinued at this stage, but living material was transported to the Zoölogical Laboratory of the University of Michigan. The temperature during transportation was regulated with ice. After their arrival at the laboratory the embryos were kept in filtered water aerated with an aspirator, in dishes partly immersed in cool running water. The loss both during and after transportation was very slight.

Four Weeks' Embryos. — Embryos a month old have attained a length of about 20 mm. The eyes are prominent and pigmented; the entire dorsal side of the body is well covered with black pigment, though the pigment is far from being as dense as in an *Amblystoma* or a frog at a corresponding stage of development. Lateral line sense organs can be distinguished. The three pairs of external gills are well fringed and pink with blood; the blood corpuscles are large and may be easily observed with a hand lens. The vitelline vein, now very prominent, has shifted to a position along the lower part of the left side of the yolk sac. A conspicuous red spot marks the position of the heart.

Spontaneous movements (exercise movements) now occur. These consist of jerking the head from side to side; wriggling; reversal of the laterally curved position of the body by turning over; swimming movements in which the embryo butts against the envelope and subsides; swimming in a circle. Embryos removed from the capsule at this stage make practically the same movements; they are unable to progress in a straight line and incapable of prolonged swimming movements.

Hatching. — Embryos collected when about three weeks old and kept in the laboratory at a temperature averaging about 13° C., began to hatch on October 17, about six weeks after the eggs were probably laid. Nearly all were hatched by October 24. At this time the average length was about 25 mm. The appearance of the embryos just previous to the hatching is shown by Fig. 8.

Before the hatching period, the envelopes become much softened and considerably enlarged by the absorption of water, making room for the growing embryo. The latter sometimes escapes by pushing its way through the envelope, leaving a small round hole; sometimes apparently by tearing or bursting the envelope by means of its wriggling movements.

In its natural environment the hatching of the embryo is perhaps delayed a little by the slightly lower temperature, but the climatic conditions are such that it seems at least certain that hatching occurs at some time during the fall.

According to Kerbert ('04), the eggs of *C. japonicus*, kept at an average temperature of 13° C., hatched in from 52 to 68 days,

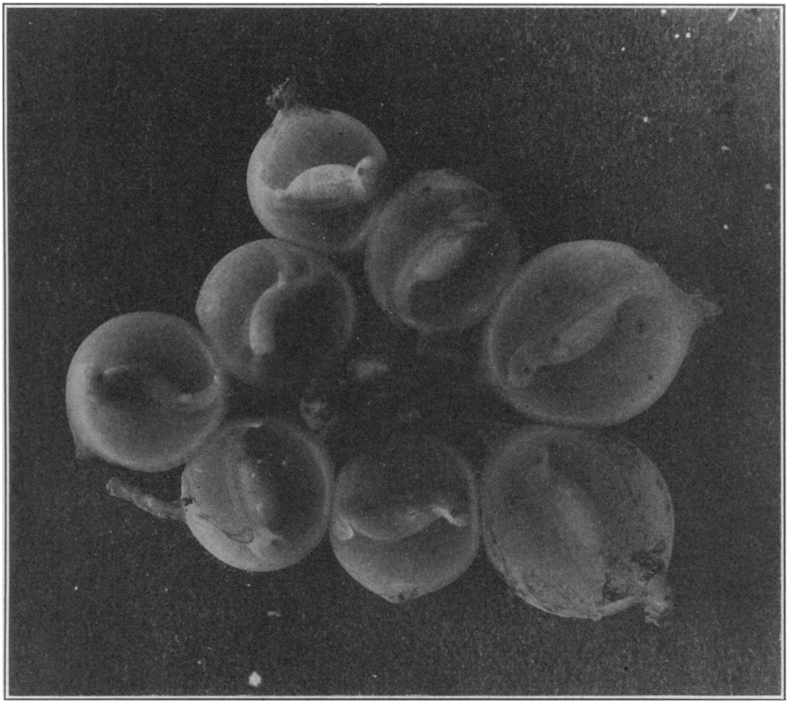


FIG. 8. Embryos of *Cryptobranchus alleghenienis*, ready to hatch, about six weeks old. Natural size.

and at the time of hatching the embryos were 30 mm. long. Since the extreme length of the adult *C. japonicus* is 159 cm. (Gadow, '01) as compared with 56 cm. for *C. alleghenienis*, there is far from being a corresponding difference in the size of the embryos at the time of hatching.

IV. The Larva.

A. *Early Stages Studied in the Laboratory.*

The Newly Hatched Larva. — At the time of hatching the larva (see Fig. 9) retains a large yolk sac. The dorsal surface is well

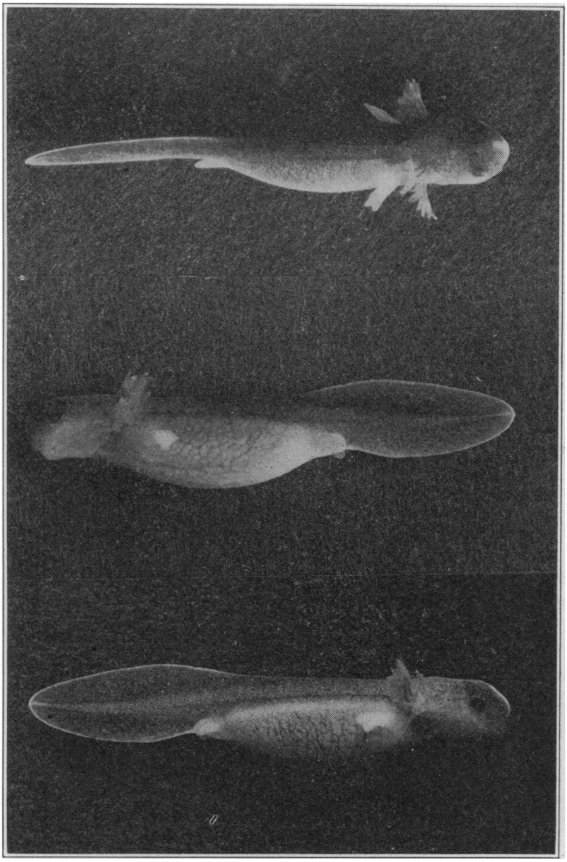


Fig. 9. Newly hatched larva of *Cryptobranchus alleghenienisis*, 25 mm. long, photographed while living. × 2½.

pigmented, but the larva is pale as compared with amphibians that live exposed to the light. The ventral surface is lacking in pigment, leaving the abdominal region yellow from the presence of yolk and the throat region white and nearly transparent. The heart can be readily observed without dissection. The vitelline vein is very prominent. The anterior limb rudiment is provided with two toes. The somites are plainly visible in most specimens, but do not show in the figure. The mouth opening is large and ventrally situated, and the mouth cavity is well developed. The eyes are more prominent than in the adult. The dorsal and lateral surfaces, especially of the head, are thickly studded with small round white spots, presumably sense organs and mucus glands.

On account of the large yolk sac, the larva habitually lies on its side, turning occasionally from one side to the other. When the larva is placed upon its back, the righting reaction, aided as it is by the ballast of yolk, is very quick. The newly hatched larva is able to swim rapidly in a straight line for a short distance, using the tail as a propeller.

The larvæ avoid the light and are positively rheotactic. Under natural conditions, the result of these two modes of behavior probably is that the larvæ remain in the nest.

Aeration of the blood is afforded, not only by the external gills, but by the capillaries which lie close to the surface all over the body. The tail may be of especial importance in respiration, for here, as in the external gills, the capillary network lies in close proximity to the water on both sides.

At the time of hatching, patches of cilia are scattered over practically the entire surface of the body, but are especially numerous on the gills. Their beat is backward, and they create a current of water, subservient to respiration, which is particularly strong in the vicinity of the gills. The presence of cilia on the ectoderm of Amphibian embryos has been remarked by various writers (see Assheton, '96).

The Month-old Larva. — In larvæ about a month after hatching (see Fig. 10), there was noted a marked increase in length, principally due to the development of the tail. The larvæ now measure from 30 to 35 mm. There is also a rapid elongation and development of the front limbs, which now have four toes. The form and position of the front limbs adapt them for use as paddles. The posterior limbs develop more slowly, are relatively short and have but three toes distinctly visible, though in some cases rudiments of the fourth and even the fifth are present. The yolk sac is reduced enough so that the larva no longer lies on one side. The mouth opening is now only slightly ventral. Pigmentation is greatly advanced, and extends to the external gills; when viewed from above the larva is now nearly black. The ventral side remains white and nearly transparent in the throat region and yellow in the region of the abdomen or yolk sac. The heart is still visible, and the course of the blood through it may be readily followed. The vitelline vein, now lying almost in the median line ventrally, shows signs of degeneration.

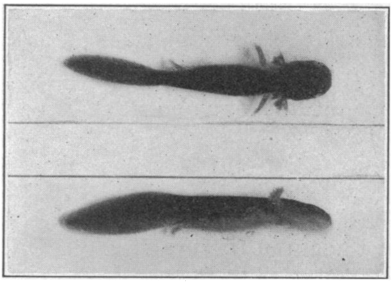


FIG. 10.

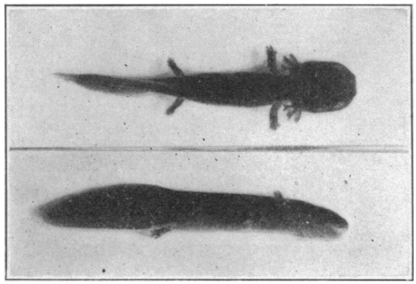


FIG. 11.

FIGS. 10 and 11. Photographs from living material, showing early stages in the development of the larvæ of *Cryptobranchus allegheniensis*. Natural size.

FIG. 10. Larvæ one month after hatching. Length 35 mm.

FIG. 11. Larva ten weeks after hatching. Length 40 mm.

At this age the larvæ are more active swimmers than the adults. The front limbs assist in starting by a quick simultaneous backward stroke.

Ciliation of the epidermis is now found only on the gills, where a strong eddying current of water is produced. No water current in at the mouth or nares and out through the gill slits could be detected.

At this stage shedding of the cuticle was observed for the first time, and was quite general; the water of the aquaria became cloudy with portions of detached epidermis.

Ten Weeks' Larva. — (See Fig. 11.) There is a slight increase in length since the first month; the larvæ now range from 35–40 mm. The limbs are better developed, possess the full number of toes, and are used in walking in the same manner as in the adults. The limbs are broad and flat, and are used as paddles in swimming at a moderate rate of speed. After fixation the somites show very distinctly.

The yolk sac is greatly reduced, and in some specimens the abdomen presents a shrunken appearance. The vitelline vein is no longer visible. The larvæ seize small pieces of beef offered to them, but do not swallow them.

Six Months' Larva. — Larvæ six months after hatching measure about 40 mm. From the third to the sixth month the increase in length is very slight, but the larva becomes much stouter in structure.

After the fifth month the larvæ not only seize small pieces of raw beef moved along a little to one side of the head, but, to a limited extent, swallow and retain these morsels. The presence of feces in the water indicates that some of the meat is digested.

In larvæ of this age fixed in Tellyesnicky's fluid and preserved in alcohol, the lateral line organs are quite conspicuous; their distribution can readily be made out with the naked eye.

Neither the larvæ of this nor of earlier stages have been observed to come to the surface for air.

The course of larval development described above may be somewhat slower under natural conditions on account of lower temperature. During the period under consideration the temperature of the aquaria ranged from 13° to 9° C., while that of the stream from which the specimens came ranged from 10° to 5° C. It is very probable that the larvæ hibernate in the nest, and perhaps do not emerge until late in the following spring. I have found clusters of 35 mm. *Necturus* larvæ late in August, occupying what was apparently their original nest.

At the time of writing a considerable number of larvæ are being kept alive in the laboratory, and it is hoped that some of them may be reared to the adult condition.

B. *Later Stages Studied in the Field.*

During August of the past summer search was made for larvæ in their natural environment. A few larvæ were found beneath small flat stones in running water only three or four inches deep.

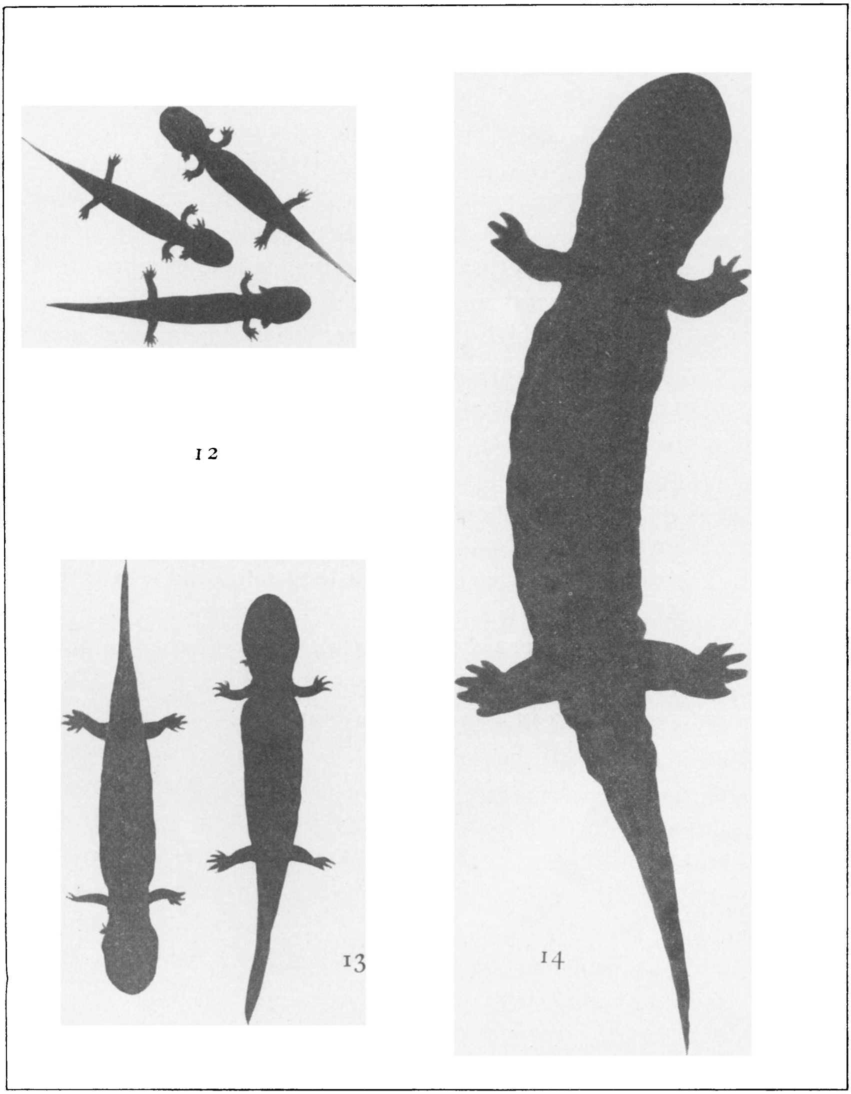
The Year-old Larva.— The smallest specimens obtained (see Fig. 12) were about 7 cm. long. Four specimens were found measuring as follows; 6.4 cm., 6.8 cm., 7.0 cm., 7.3 cm. These were presumably hatched during the preceding autumn. The external gills are retained, though evidently in a somewhat degenerate condition. The legs are well developed. The mouth opening is terminal, not ventral. The tail is proportionally smaller than in specimens ten weeks old; the ratio of length of tail to entire length is 1 : 2.5 in the case of the year-old larva, and 1 : 3 in the ten-weeks' larva. The body is plump as compared with the adult, the somites show distinctly, and the lateral folds are very slightly developed. There is a conspicuous gular fold not present in the adult. The color of the dorsal and lateral surfaces is a very dark brown, almost black, so that the irregular black spots which are present do not show in the photograph. After preservation in formalin the ground color becomes lighter and of a bluish tint, and the black spots show more distinctly. A few scattering inconspicuous yellow spots are also present. The ventral surface is considerably lighter in color.

These larvæ are more active than the adults, and are extremely sensitive to shocks and jars. They were never observed to come to the surface for air.

The Two-year-old Larva. — (See Fig. 13.) Two specimens were found, measuring respectively 12 cm. and 12.3 cm. These differ from the year-old larvæ in the small size of the external gills, in the absence of the gular folds, the slightly greater development of the lateral folds, and in the absence of visible somites, though the lateral folds are metamerically notched. The ground color is a trifle lighter, so that the black spots are more clearly seen; less conspicuous yellow spots are also present. No stages intermediate between these and the 7 cm. larvæ were obtained, and it seems probable that they represent the second year of larval development.

One of these specimens ate, soon after being captured, a large *Corydalis* larva. Another specimen, when placed in quiet water, regurgitated a partly digested 6 cm. larva of its own kind.

As in the younger stages, these specimens were not observed to come to the surface for air; however, the evidence on this point is not conclusive.



FIGS. 12–14. Larval and post-larval stages of *Cryptobranchus alleghenienis*, ½ linear reduction. From living specimens.

FIG. 12. Larvæ taken August 14, photographed August 17, 1906. Length 6.4 cm., 6.8 cm., and 7.0 cm. respectively.

FIG. 13. Larvæ taken August 14, photographed August 17, 1906. Lengths 12.0 cm. and 12.3 cm. respectively. Reduced external gills are present on both sides.

FIG. 14. Young *Cryptobranchus* 26.7 cm. long.

V. Post-larval Development.

A series of sizes intermediate between the 12 cm. larvæ and the adults was obtained. Six specimens taken during a single week in August measured as follows: 14 cm., 16.2 cm., 18.3 cm., 21 cm., 21.5 cm., 26.7 cm. All these had lost their external gills, but were sexually immature. The lateral folds show increased development throughout the series. The coloration is about the same as that of the young adult; Fig. 14 will serve to show the general appearance of the specimens ranging from 16 to 35 cm., in which the spots are more conspicuous than in either very young or very old specimens.

Sexual maturity is attained with a length of about 34 cm., and probably requires three or four years from the time of the fertilization of the egg.

In conclusion, I take pleasure in acknowledging my indebtedness to Professor Jacob Reighard for training in field work without which it would have been impossible for me to conduct studies of this kind far from the advantages of a laboratory, and to Dr. O. C. Glaser, under whose direction work was continued at the university, for invaluable encouragement and advice.

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